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STUDY OF A LOWER CRETACEOUS ACTINOPTERYGIAN (CLASS PISCES) *COOYOO AUSTRALIS* FROM QUEENSLAND, AUSTRALIA

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ABSTRACT

The Lower Cretaceous actinopterygian fish *Xiphactinus australis* Woodward, 1894 is redescribed from new material. Comparisons of this taxon with other ichthyodectid genera, *Xiphactinus, Ichthyodectes, Cladocyclus* and *Gillicus*, shows it is sufficiently distinct to warrant recognition in a separate genus, *Cooyoo* gen. nov.. In addition *C. australis* is shown to be more closely related to *Ichthyodectes* than *Xiphactinus*.

INTRODUCTION

Woodward (1894) described an isolated partial teleost skull from Lower Cretaceous marine sediments of Queensland and identified it as the new species, *Portheus australis*. *Portheus* was later shown by Hay (1897) to be a junior synonym of *Xiphactinus*, a conclusion followed by most subsequent workers.

Since Woodward's (1894) description, no further work has been carried out on this species. During this time, the Queensland Museum has acquired a number of excellent specimens of this fish, including an almost complete skeleton, several well preserved skulls and a neurocranium, as well as numerous pieces of vertebrae, partial crania, jaws and skeletal fragments. The material, collected from marine sediments of the Hughenden, Richmond and Boulia areas of Central Queensland, forms the basis for the current revision and allows for a more complete description and identification of the species.

Detailed comparison is made with four ichthyodectid genera: *Xiphactinus* Leidy, 1870, *Ichthyodectes* Cope, 1870, *Cladocyclus* Agassiz, 1841 and *Gillicus* Hay, 1898. This indicates that the Queensland species requires separate generic status.

Relationships with the Ichthyodectidae have been discussed by several workers, namely Bardack (1965), Bardack and Sprinkle (1969), Cavender (1966), Nelson (1973), Taverne (1973, 1974) and, most recently, Patterson and Rosen (1977). The classification of Ichthyodectiformes proposed by Patterson and Rosen (1977) will be followed:

O. ICHTHYODECTIFORMES Bardack and Sprinkle, 1969

S.O. ALLOTHRISSOPOIDEI Patterson and Rosen, 1977

F. Allothrissopidae Patterson and Rosen, 1977
Genus *Allothrissops* Nybelin, 1964

S.O. ICHTHYODECTOIDEI Romer, 1966

F. Ichthyodectidae Crook, 1892
Ichthyodectes Cope, 1870, *Xiphactinus* Leidy, 1870, *Gillicus* Hay, 1898, *Cladocyclus* Agassiz, 1841, *Eubiodectes* Hay, 1903, *Proportheus* Jaekel, 1909, *Chriocentrites* Hackel, 1849, *Thrissops* Agassiz, 1833, *Spathodactylus* Pictet, 1858, *Cooyoo* gen. nov.

F. Saurodontidae Cope, 1871
Saurodon Hays, 1930, *Saurocephalus* Harlan 1824

SPECIMEN DESIGNATIONS

QMF — Queensland Museum specimen, GSQ — Geological Survey of Queensland specimen.

Abbreviations in Figures

Terminology follows Bardack (1965)

Ang.	angular
Boc.	basioccipital
bpt. pr.	basipterygoid process
Bsc	basisclerotic
Bsp.	basisphenoid
Dent.	dentary
Ect.	ectopterygoid
eff. ps. a.	foramen for efferent pseudobranchial artery
Epo	epiotic
Eth.	ethmoid
Exo.	exoccipital
f.m.	foramen magnum
Fr.	frontals
Hym.	hyomandibular
hym. f.	hyomandibular fossa
inf. f.	infundibular fossa
Int.	intercalar
lat. head v.	lateral head vein
lat. temp. f.	lateral temporal fossa
Max.	maxillary
Mes.	mesopterygoid
Mpt	metapterygoid
Op.	operculum
Pal.	palatine
Par.	parietal
Pas.	parasphenoid
Pmx.	premaxillary
Pop	preoperculum
Pro.	prootic
pro. br.	prootic bridge
ptm. f.	post-temporal fossa
Pto.	pterotic
Qu.	quadrate
Ra.	retroarticular
Sclr.	sclerotic
se. f.	Subepiotic fossa
Soc.	supraoccipital
Sph.	sphenotic
IX	foramen for glossopharyngeal nerve
X	foramen for vagus nerve

Superorder TELEOSTEI
Order ICHTHYODECTIFORMES Bardack and Sprinkle, 1969
Suborder ICHTHYODECTOIDEI Romer, 1966
Family ICHTHYODECTIDAE Crook, 1892

Genus **Cooyoo** gen. nov.

Diagnosis

Medium-sized ichthyodectid teleost (single complete individual 1.1 m). Supraoccipital crest rises above the dorsal surface of the neurocranium at a mean angle of 15°, significantly lower than in both *Xiphactinus* (30°) and *Ichthyodectes* (39°). Fused parietals unornamented. Frontals possess raised, medially concave ridges originating at anterior base of parietal hump, diverging to form part of dorsolateral margin of brain case; anteriorly, the ridges converge to complete an oval-shaped ring bounding anterodorsal surface of neurocranium; between the ridges, frontals are smooth and rise to a peak at midline; frontals also exhibit laterally directed, triangular-shaped shelf. No ridges have been observed on the frontals of *Xiphactinus*; in *Ichthyodectes* ridges are present, but are medially convex.

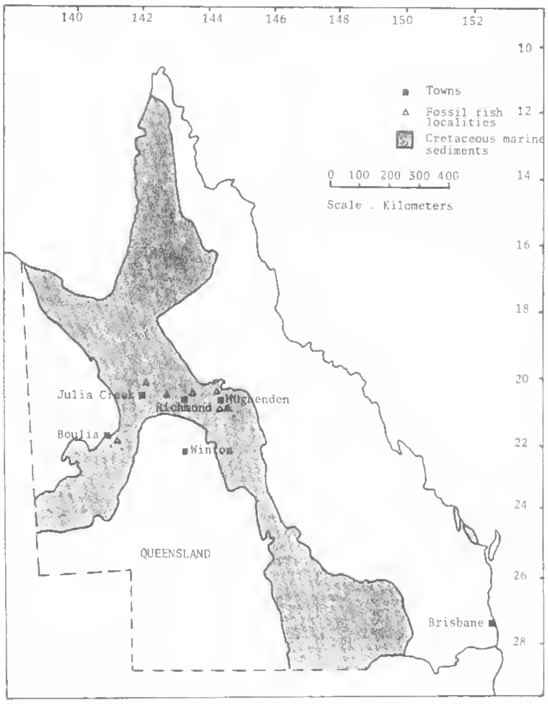

Fig. 1: Localities from which *Cooyoo australis* specimens have been collected.

Sphenotics project laterally tapering to truncated points; sphenotics directed lateroventrally in *Xiphactinus* and anteroventrally in *Ichthyodectes*.

Large, ventrally directed hyomandibular fossa lies obliquely across lateral surface of neurocranium, spanning the sphenotic, prootic, pterotic and intercalar; its posterior portion is obscured by a wing of pterotic. Hyomandibular fossa is orientated horizontally in both *Xiphactinus* and *Ichthyodectes*. Located directly below the hyomandibular fossa is large, rhomboidal, subtemporal fossa, posteroventral margin of which is formed by slanted, prootic-intercalar bridge.

Above hyomandibular fossa on pterotic is a depression forming the lateral temporal fossa; dorsal margin of this fossa rises from midpoint of hyomandibular fossa, extending upward in an arc ending on frontals.

Teeth are medium to small (mean height 4 mm); size range within a jaw is low. In *Xiphactinus* the teeth are large (1-4 cm) and variable in size. In *Ichthyodectes* the teeth have a mean height of 8 mm and show little size variation.

Premaxillary basically rectangular, elongated dorsoventrally; its dental margin is curved and bears six alveoli. *Xiphactinus* has an ovate premaxillary with a straight dental border; 5-6 alveoli are present. In *Ichthyodectes* the premaxillary is rhomboidal or ellipsoidal in profile with a mean number of 6.6. alveoli.

RANGE

All material with detailed locality information has been collected from either the Toolebuc Formation or Allaru Mudstone, both of which are Lower Cretaceous (Albian) age (Day *et al.*, 1983), not as suggested by Bardack (1965) Upper Cretaceous.

ETYMOLOGY

The name means fish in the Pooroga language spoken by the Jarambali Aborigines who lived in the Upper Flinders, Hughenden and Dutton River districts (Curr and Curr 1887).

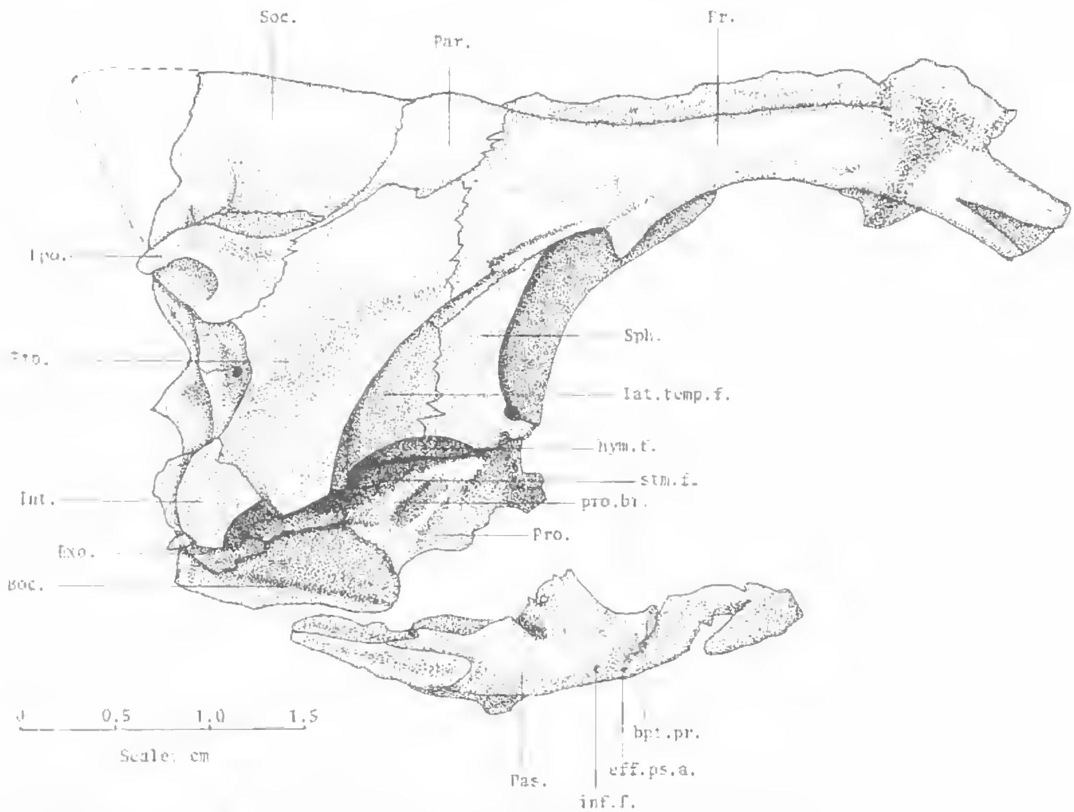

FIG. 2: *Cooyoo australis*. Lateral aspect of neurocranium from specimen QMF 12325.

Cooyoo australis (Woodward, 1894)

Portheus australis Woodward, 1894, pp. 444–7, pl. 10; Longman, 1913, pp. 95–4; Wade, 1930, p. 143; David, 1950, p. 499; Hills, 1958, p. 99.

Xiphactinus australis (Woodward, 1894); Bardack, 1965, p. 54; Hill, Playford and Wood, 1968, pl. K XII (1); Long, 1982, p. 71.

MATERIAL

Holotype, GSQ2445 Portion of upper and lower jaw, Clutha Station, near Hughenden, 5 km from Home station on Gidgery Creek. Fm.: Allaru Mudstone. Age: Lower Cretaceous, Albian. Referred specimens all of Albian age: QMF354, partial skull, Hughenden, near Flinders River, QMF1016, skull, six miles northeast of Richmond; QM F2581, vertebrae and ribs, 'Lydia Downs', Nelia; QMF6346, skull and vertebrae, 'Laura Downs', Julia Creek, at M.R. 465493 Julia Creek 1:125,000. Allaru Mustone; QMF9466, skull, Stuart Creek, Hughenden; QMF9468, skull, Dinga Ding Station, near McKinlay, Allaru Mudstone; QMF9469, skull, 'Boree Park', near Richmond; QMF9471, vertebrae, 'Dinga Ding Station', near McKinlay, Allaru Mudstone; QMF9472, skull, 'Dinga Ding Station', near McKinlay, Allaru Mudstone; QMF12325, neurocranium, 'Warra Station', near Richmond, Toolebuc Formation; QMF12327, skull, fin and vertebrae, Pelican Bore, Stewart Creek, 'Dunraven Station', near Hughenden, Toolebuc Formation; QMF12710, partial skull, 'Arrara Station', near Hughenden North-west or Weather Paddock, Allaru Mudstone; QMF12711, skull, Mountain Creek, 'Redcliffe Station', near Hughenden, Allaru Mudstone.

DIAGNOSIS

As for the genus.

DESCRIPTION

While most of the skeleton of the species is known, certain cranial elements — vomer, orbital bones, supramaxillary bones — and certain caudal elements — pectoral girdle and pelvic and caudal fins have not, as yet, been recorded.

NEUROCRANIUM (Figs 2–4): incomplete, with the vomer unknown and ethmoid and parethmoid only partially known. Basically wedge-shaped, with the base formed by stout parasphenoid and dorsal roof by ethmoid, frontals, parietals and supraoccipital.

SUPRAOCCIPITAL (Figs 2–4, 6): forms triangular-shaped crest rising from posterior margin of parietals above dorsal surface of neurocranium at an angle of approximately 15° (5 specimens); viewed laterally, posterior margin of crest appears concave; viewed posteriorly, supraoccipital crest forms dorsal pinnacle, crowning neurocranium, from which it extends ventrally to contribute to formation of large subepiotic fossae; at base of crest, supraoccipital expands laterally to join epiotics.

EPIOTIC (Figs 2–4, 6): crests approximately a quarter height of supraoccipital crest; supraoccipital — epiotic suture runs along median side of epiotic ridge, just below its crest; epiotics also form dorsal corners of the posterior surface of neurocranium and contribute to formation of large subepiotic fossae and post-temporal fossae.

PARIETALS (Figs 2, 3, 6): fused medially, lying anterior to supraoccipital crest; relatively small bones forming a dome at midline of dorsal neurocranial surface. They extend posteriorly around the anterior base of supraoccipital crest and carry anterior extensions of epiotic crests; dorsally, surface unornamentated.

FRONTALS (Figs 2, 3, 6): large, extending from anterior parietal margins to cover nearly a third of dorsal neurocranial surface. Each bears prominent ridge originating at anterior margin of parietals, just below dorsal midpoint of neurocranium; these gradually diverge anteriorly, curving along dorsolateral margin of frontals, roofing orbits and then reconverging anteriorly; between ridges,

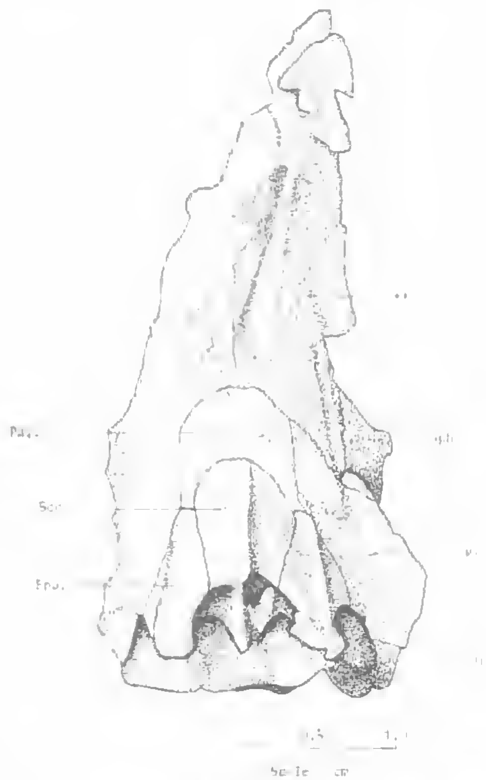

FIG. 3: *Cooyoo australis*. Dorsal aspect of neurocranium from specimen QMF 12325.

smooth frontals rise gently to form broad ridge at their common suture; each exhibits laterally directed triangular shelf, midway along dorsolateral margin; anterior margins of frontals obscured or damaged. The anterior border of the frontals is probably formed by the ethmoids and parethmoids.

ETHMOIDS (Fig. 6): imperfectly known; suture with frontals obscured but, anteriorly, they appear to exhibit beak-like rounded margin; at anterolateral corner of ethmoid is ventrally directed process appearing to articulate with dorsal surface of palatine head; anteroventrally, each contributes to deep lateral fossa, probably to accommodate premaxillary ligaments.

PARETHMOIDS: lie ventral to ethmoids and frontals; each contributes to lateral fossa; they also form lateral wall of nasal capsule and portion of anterior margin of orbit; anteroventral surface forms large concave condyle articulating with saddle-shaped surface of palatine head.

SPHENOTICS (Figs 2, 3, 6): situated at posterior ventrolateral corner of frontals; posteriorly, they meet pterotics and ventrally are bound by prootics; they exhibit laterally directed projection tapering to truncated point; posteroventral portion of sphenotic forms anterolateral corner of hyomandibular fossa.

HYOMANDIBULAR FOSSA (Fig. 2): large, elongate, opening ventrally, running obliquely across almost entire length of otic section of neurocranium, spanning four separate bones;

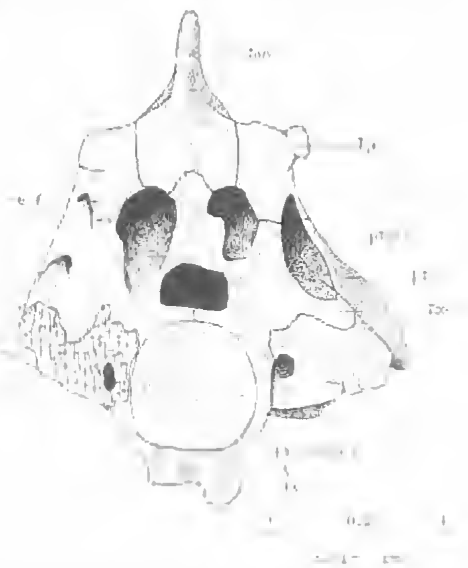

FIG. 4: *Cooyoo australis*. Posterior aspect of neurocranium from specimen QMF 12325.

sphenotic and prootic form elevated anterior corner of fossa, intercalar forms lower posterior corner, while pterotic comprises bulk of fossa and laterally obscures most of its posterior portion.

PTEROTICS (Figs 2, 3, 6): large, covering much of lateral surface of brain case; dorsally, bounded by parietal and epiotic, ventrally by prootic, posteriorly by intercalar and anteriorly, extend to meet sphenotic ventrally and frontal dorsally; as well as containing most of hyomandibular fossa, pterotics also bear lateral temporal fossa and roof of subtemporal fossa; dorsal margin of lateral temporal fossa forms an arc running from midway along ventral margin of pterotic, forward to posteroventral corner of frontals; pterotics also forms at least half lateral margin of posterior surface of the neurocranium; combined with epiotic and exoccipital bones, contributes to large, posterior, post-temporal fossa.

SUBTEMPORAL FOSSA (Fig 2): large, well developed and rhomboidal; roof formed by the pterotic, but mostly contained by prootic and intercalar; the prootic and intercalar form bridge lying obliquely across posteroventral margin of fossa.

INTERCALAR (Figs 2, 3): large, forming posteroventral neurocranial corner; bounded ventrally by exoccipital and anterodorsally by pterotic; posteriorly, meets exoccipitals; together forming foramen for vagus and glossopharyngeal nerves and lateral head vein.

PROOTIC (Figs 2-4): anterior to intercalar and basioccipital bones, forming most of anterodorsal portion of subtemporal fossa; covers nearly half lateral face of brain case and incorporates two foramina, one leading into prootic canal and other for hyomandibular branch of 7th nerve.

BASIOCCIPITAL (Figs 2, 4): positioned posterior to prootic but ventral to intercalar, forming posteroventral corner of brain case; lateral surface of basioccipital markedly concave to accommodate branch of swim bladder.

EXOCCIPITALS (Figs 2, 4): form most of ventral portion of posterior face of neurocranium; laterally they are barely visible, sandwiched between intercalar dorsally and basioccipitals ventrally; posteriorly, contribute to subepiotic fossa and together form foramen magnum; fused to medial ventral surface is half a vertebra.

PARASPHENOID (Figs 2, 6): strong, elongate, lying ventral to basioccipital and prootic, forming base of brain case; transversely, beneath orbit it has sharply convex dorsal surface and gently convex ventral surface; beneath brain case, parasphenoid divides posteriorly into two arms, triangular in cross section with concave lateral surfaces; arms taper posteriorly, terminating in points at posterior end of brain case; stout basipterygoid processes present, extending anterolaterally just anterior to otic section of neurocranium; anterior portion of parasphenoid not preserved and relationship with vomer cannot be ascertained; parasphenoid flexes upward at junction of otic and orbital sections of neurocranium; with mean angle of flexure approximately 149° (3 specimens).

PREMAXILLARY (Fig. 6): rarely preserved, suggesting that ligamentous attachments not very strong; a relatively large, robust bone sub-rectangular in outline; oral border curved, with six alveoli, at least four bearing teeth.

MAXILLARY (Fig. 6): long, fairly shallow, narrowing posteriorly; anterodorsal margin with hammer-like condyle articulating with malleolar head of palatine; anterior to condyle, maxillary shows another, smaller condyle abutting a facet formed by vomer and ethmoid; ventral edge of maxillary essentially straight, containing variable number of teeth (Table 1); teeth may occur in every alveolus or every second alveolus; Table 2 shows range in tooth size and number found; teeth not very large (mean 4 mm) and, within an individual, show only small range in height; lateral maxillary surface flat, showing little ornamentation, except just below dorsal surface maxillary where distinct groove accommodated ventral margin of supramaxillary bones; posterior end of maxillary not well preserved, but exhibits dorsal swing with ventral margin resting in groove in quadrate.

SUPRAMAXILLARY: bones thin, fragile, poorly preserved; shape difficult to determine, probably comprising smaller, almost ovoid posterior bone and larger, rectangular, anterior bone, dorsal

TABLE 1. Number of alveoli and tooth size observed in the maxillary of specimens of *Cooyoo australis*. The size of the sample limits the amount of interpretation possible, however the size of the standard deviations clearly indicates how little tooth size varies in a single specimen.

MAXILLARY							
Specimen	Alveoli No. Left	Alveoli No. Right	Teeth No. Left	Teeth No. Right	No. of complete teeth measured	Mean Size (cm)	SD
QMF10209	27+ (anterior damaged)	38	14+ (anterior damaged)	26	17	0.369	±0.155
QMF1016	38	32	28	22	All teeth broken		
QMF6346	34	not visible	23	not visible	8	0.409	±0.05
QMF12327	34	not visible	17	not visible	10	0.45	±0.107

TABLE 2. Number of alveoli and size of teeth observed in the dentary specimens of *Cooyoo australis*.

DENTARY					
Specimen	Alveoli No. Left	Alveoli No. Right	Teeth No. Left	Teeth No. Right	Sizes (cm)
QMF10209	Tooth row obscured by Maxillary				
QMF1016	20	posterior end broken	11	11+	0.75,0.94,0.86 most teeth broken
QMF6346	Most teeth obscured or broken				0.9,0.54,0.59,0.72
QMF12372	Most teeth obscured or broken				0.8,0.36,0.49,0.52
GSQ2445	Most teeth broken				0.99,1.08

margin of which seems to be convex.

DENTARY (Fig. 6): fairly stout, deep, bearing single row of medium-sized teeth (mean 7 mm); teeth almost uniform size, except in QMF12327 where first few teeth larger and broader than rest; dental margin rises to peak just before posterior end of bone; posterior to peak, margin plunges steeply downward to anterodorsal margin of angular; angular then flexes dorsally to articulate with quadrate; most of ventral margin of dentary straight, but flexes dorsally below angular; no internal view of dentary available. Table 2 shows ratio of mandibular length to depth; ratio difficult to measure because of poor preservation of bones and comparison with other genera should be treated with caution.

HYOMANDIBULAR (Figs 5, 6): largest of hyopalatine bones; dorsally, 'dumbell'-shaped head articulates with hyomandibular fossa; posterior hyomandibular margin forms gently curving raised rim, edging posterior margin of skull and articulating with preopercular; anterior to rim, hyomandibular markedly concave; concave portion covered by postorbitals.

METAPTERYGOID (Figs 5, 6): anterior to hyomandibular; large, right-angle shaped element, bounded by quadrate posteroventrally, ectopterygoid anteroventrally and mesopterygoid anteriorly; it makes no contribution to boundary of orbit, formed by the palatine, mesopterygoid and hyomandibular.

MESOPTERYGOID (Figs 5, 6): comparatively small, wedged between hyomandibular and palatine, and dorsal to metapterygoid; despite small size, it forms almost half margin of orbit; at junction with hyomandibular is groove for basipterygoid process.

PALATINE (Figs 5, 6): lies anterior to mesopterygoid; it possesses distinct malleolar head; dorsal surface of head peaked, articulating with ventrally grooved parethmoid; ventral palatine surface concave accommodating condyle on dorsal edge of maxilla.

ECTOPTERYGOID (Figs 5, 6): ventral to palatine, anterior to metapterygoid and dorsal to quadrate; elongate, forming ventral margin of

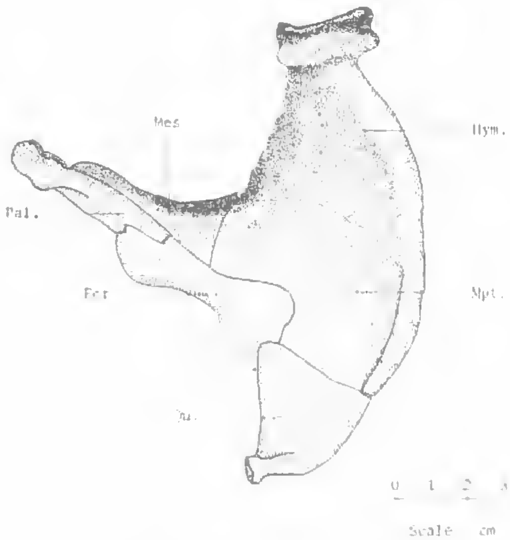

FIG. 5: *Cooyoo australis*. External view of hyomandibular bones. Reconstructed based on specimens; QMF 1016, QMF 12327, QMF 12711.

TABLE 3. Measurements of maxillary and dentary length and depths observed in specimens of *Cooyoo australis*.

Specimen	Maxillary		Dentary	
	Length (cm)	Depth (cm)	Length (cm)	Depth (cm)
QMF10209	6.2 (approx)	posterior condyle obscured	5.27	3.18
QMF1016	8.46	1.34	5.5	3.75
QMF6346	8.54	1.98	5.34 (?) obscured	4.3 (?)
QMF12327	9.56	1.87 (approx)	6.71 (?) obscured	4 (?)

Maxillary length measured from posterior margin of premaxillary to last alveolus.
Maxillary depth measured at posterior condyle.
Dentary length of alveolar border.
Dentary depth measured at coronoid process

hyomandibular apparatus; anteriorly, it has interdigitating suture with palatine; posterior margin and its relationship with hyomandibular difficult to determine as usually broken and distorted.

QUADRATE (Figs 5, 6): articulates with ventral margins of ectopterygoid, metapterygoid and hyomandibular; triangular, with ventral apex forming articulating head for the jaws; posterior margin of the maxilla lies in groove on this condyle and angular portion of lower jaw articulate with it.

SYMPLECTIC: small, splinter-like lying near posterior margin of quadrate.

CIRCUMORBITALS: not preserved in most specimens and, at best, only partially preserved; fragmentary evidence indicates probably six circumorbital plates - dermosphenotic, two supraorbitals, lacrymal, infraorbital and a large postorbital which, when preserved, mask much of hyopalatine bones.

SCLEROTIC (Fig. 6): bones, frequently preserved; most specimens exhibit two sclerotic bones ringing eye; basal sclerotic also frequently preserved, found at bottom of eye capsule; basal sclerotic fairly thick, heavy bone exhibiting delicately spined margin and posteriorly positioned, keyhole-shaped indentation.

PREOPERCULAR (Fig. 6): elongate dorso-ventrally with an expanded ventral base bearing 13 sensory canal openings; dorsal margin appears obliquely truncated, with highest point occurring anteriorly.

OPERCULAR (Fig. 6): large, flat, abutting against posterior margin of preopercular and having a semicircular posterior margin.

Pectoral girdle and fins poorly represented. They are known only from one piece of cleithrum, a fragmentary pectoral fin and a fragmentary pelvic fin.

CLEITHRUM: robust, L-shaped.

PECTORAL FIN: exhibits nine fin rays. These are

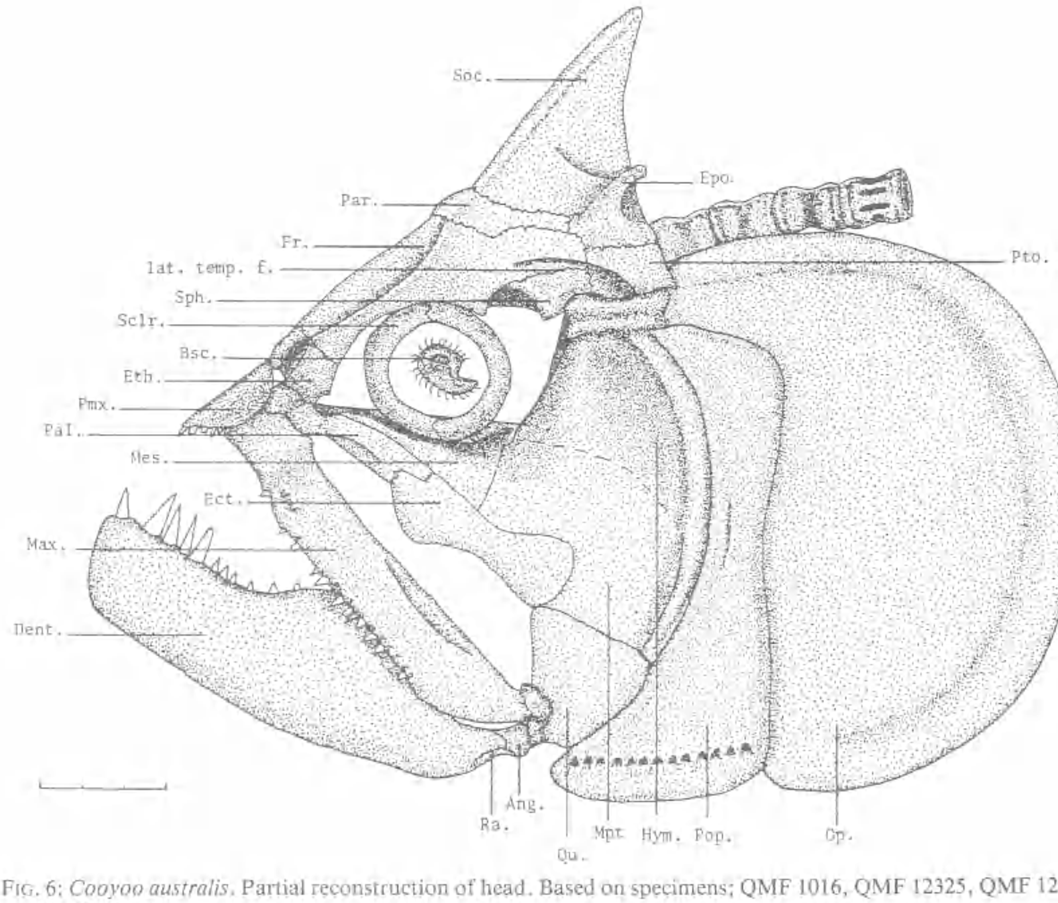

FIG. 6: *Cooyoo australis*. Partial reconstruction of head. Based on specimens; QMF 1016, QMF 12325, QMF 12327, QMF 12711.

both broad and thick, especially the most posterior ray which is almost twice the width of the others.

PELVIC FIN: is poorly preserved, exhibiting 7 broad fin rays.

A complete vertebral column and caudal skeleton has yet to be collected. It is particularly unfortunate that no tail has yet been found. The most complete skeleton possesses 65 vertebrae.

VERTEBRAE (Fig. 6): exhibit laterally a longitudinal ridge separating two deep, longitudinal grooves. This character is not apparent in the first few vertebrae which are laterally smooth; grooves also occur on the dorsal; ventral surfaces of the vertebrae receiving the heads of neural and haemal arches.

FIG 7: *Cooyoo australis* — Holotype — GSQ 2445 Portion of upper and lower jaw. Scale bar = 2cm.

REMARKS

Specimens of *Cooyoo australis* examined in this study show little variation in the morphology of bones constructing the skull. The bone shape and relative proportions appeared to remain essentially constant regardless of the overall size of the individual.

The vertebrae (QMF6139 from Station Creek, Afton Downs, Queensland) assigned questionably by Woodward (1894) to *Cladocyclus sweeti* (?) are obviously ichthyodectiform but are not considered diagnostic to a generic level.

PALAEOECOLOGY

Cooyoo australis has only been collected from sediments which are regarded as the deposits of a shallow marine environment (Day *et al.* 1983). It is found in association with marine vertebrates such as ichthyosaurs, plesiosaurs, other actinopterygians and sharks, and marine invertebrates such as ammonites, belemnites, and crustaceans. Also occurring in the deposits are the remains of terrestrial vertebrates such as dinosaurs and occasional terrestrial plants and insects which indicate proximity to the shore line.

Cooyoo australis is one of the fish most commonly collected from these sediments. This suggests that it was quite an abundant member of the ichthyofauna. Its streamlined body, powerful fins and numerous sharp teeth indicate that, like other ichthyodectiforms, it was predacious.

COMPARISONS AND GENERIC DESIGNATION

Nine genera were previously recognized as forming the family Ichthyodectidae (Patterson and Rosen 1977). These are *Ichthyodectes, Xiphactinus, Gillicus, Eubiodectes, Proportheus, Chirocentrites, Thrissops, Spathodactylus* and *Cladocyclus*. Of these, *Spathodactylus* is known only from a single poorly preserved specimen; *Chirocentrites* is possibly *Xiphactinus*; similarly *Proportheus* may be synonymous with *Cladocyclus; Thrissops* may be synonymous with *Gillicus*, and *Eubiodectes* equivalent to *Ichthyodectes* (Patterson and Rosen 1977). Because of these uncertainties, and because it is not possible to examine any of this material, *Cooyoo* will only be compared with the four accepted and fairly well known, figured and described genera, namely *Xiphactinus, Cladocyclus, Gillicus*, and *Ichthyodectes*. Comparisons will only be made at the generic level as the characters which have been used to separate species within a genus are minor. Most species are

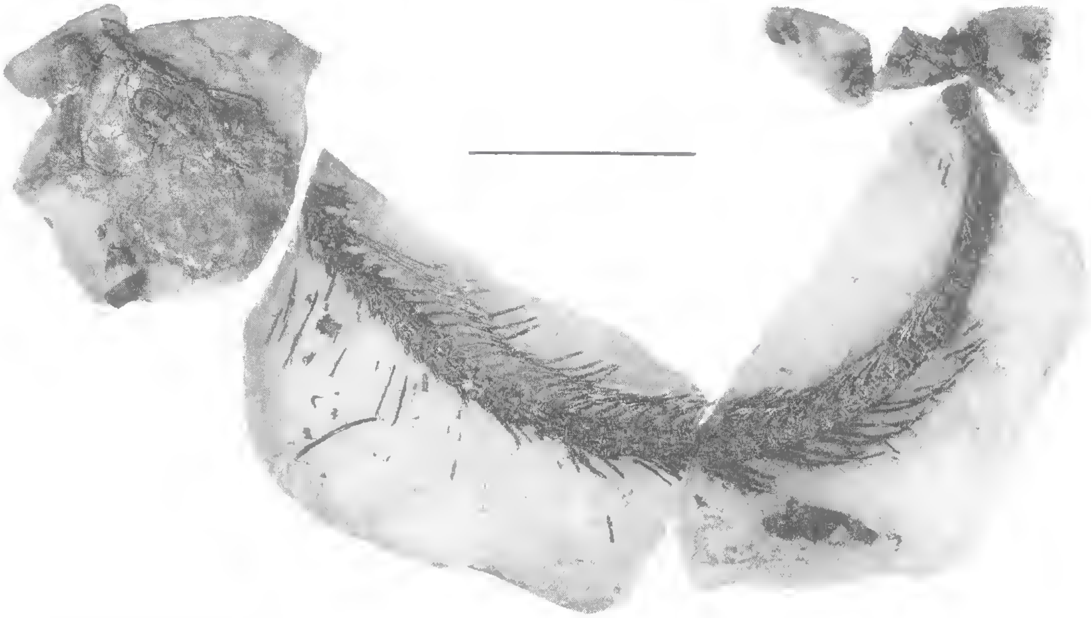

FIG 8: *Cooyoo australis* — QMF 6346. Most complete specimen collected to date. Scale bar = 20cm.

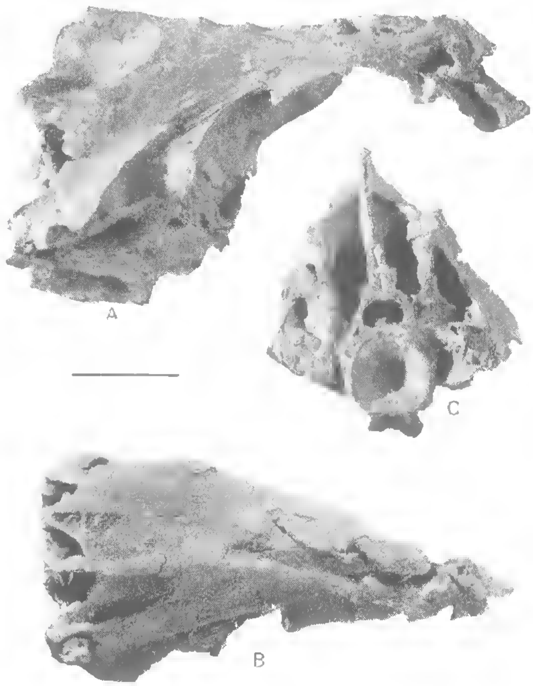

FIG 9: *Cooyoo australis* — QMF 12325 — An almost perfect neurocranium. A. Lateral view. B. dorsal view. C. posterior view. Scale bar = 1cm.

FIG 10: *Cooyoo australis* — QMF 12327 — Skull with portion of the pectoral girdle. Scale bar = 2cm.

distinguished only on geographic grounds. For example, Bardack (1965) writes 'The four species *Xiphactinus audax, X. mantelli, X. gaultinus* and *X. australis*, tentatively retained in this revision, are distinguished primarily for reasons of geographic distribution rather than for morphologic differences.'. Comparisons made herein are based on the figures and descriptions given by Stewart (1900) and Bardack (1965) for *Xiphactinus, Ichthyodectes* and *Gillicus*, and by Patterson and Rosen (1977) for *Cladocyclus*.

Although these comparisons strive to be as rigorous as possible, they are limited by the fact that only rarely are entire fish preserved or even representatives of all skeletal elements collected. For example, in the case of *Cooyoo*, almost no caudal skeletal elements have been collected and no comparisons of the tail skeletons are possible. An additional bias is that certain skeletal elements are so fragile that they are rarely preserved while the more robust predominate in the fossil material. Despite these difficulties it is considered that the material available is sufficient to define accurately the relationship of *Cooyoo* to other ichthyodectids.

Of the four most probable genera into which *Cooyoo* may have been placed, *Gillicus* and *Cladocyclus*, are obviously distinct. Main differences between *Gillicus* and *Cooyoo* are: (1) *Gillicus* possesses minute teeth less than 1mm high while in *Cooyoo* the teeth are relatively more robust with a mean height of 4mm; (2) *Gillicus* has a curved dental border, while the dental border in *Cooyoo* is straight; (3) the premaxillary of *Gillicus* contains 10–17 alveoli, considerably more than the 6 observed in *Cooyoo*; (4) in *Gillicus*, the

TABLE 4. Summary of major similarities (S) and differences (D) between *Cooyoo*, *Xiphactinus* and *Ichthyodectes*.

Feature	*Xiphactinus*	*Cooyoo*	*Ichthyodectes*
Angle of rise of Supraoccipital Crest	D 30 degrees	D 15 degrees	D 39 degrees
Proportional Height of Epiotic crests	D	S	S
Parietals Ornament Shape	 D S	 S S	 S D
Frontals Ridges Flange	 D D	 D D	 D D
Ethmoid shape	D	S	S
Sphenotic shape	D	D	D
Hyomandibular fossa orientation	D	D	D
Subtemporal fossa orientation	D	D	D
Lateral temporal fossa, size and shape	D	D	D
Basisphenoid Flexure Cross-sectional shape Division	 D 160 S D	 S 149 S D	 S 149 D D
Premaxillary Shape Number of alveoli	 D D	 D S	 D S
Maxillary Teeth size Number of alveoli	 D S	 D S	 D D

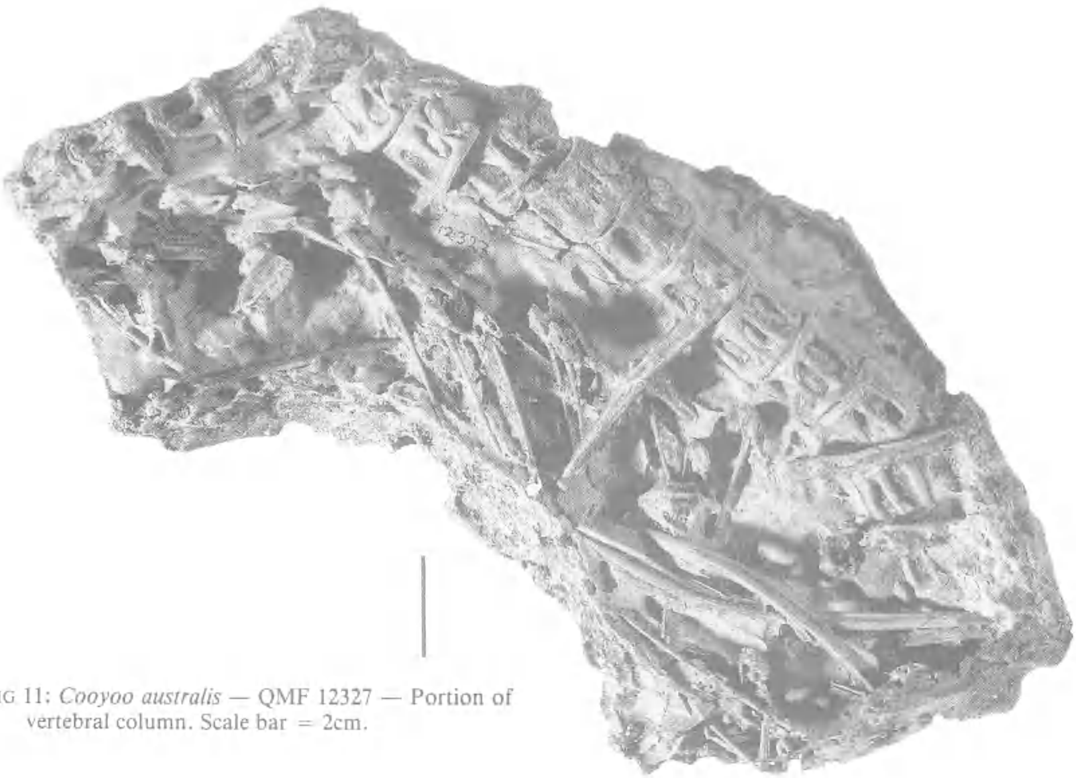

FIG 11: *Cooyoo australis* — QMF 12327 — Portion of vertebral column. Scale bar = 2cm.

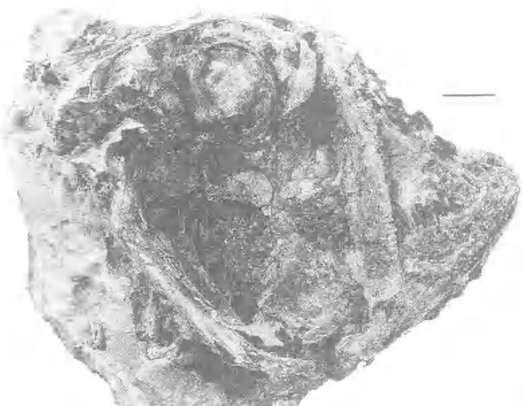

FIG 12: *Cooyoo australis* — QMF 12711 — Skull (right side) clearly showing the hyomandibular fossa. Scale bar = 2cm.

FIG 13: *Cooyoo australis* — Skull (right side). This specimen exhibits the basiclerotic plate, typical of ichthyodectiformes. Scale bar = 2cm.

parasphenoid angles sharply upward beneath the midpoint of the otic section of the neurocranium. In *Cooyoo* this flexure is very slight. In addition, the parasphenoid of *Gillicus* is quadrilateral in cross-section, while in *Cooyoo* it is triangular; (5) the lateral temporal fossa of *Gillicus* extends onto the sphenotic and is much smaller than the one observed in *Cooyoo* which extends onto the frontals; (6) in *Cooyoo* the hyomandibular fossa is tilted upward anterodorsally, opposite to that observed in *Gillicus* which tilts up posterodorsally; (7) in *Cooyoo* the hyomandibular fossa opens ventrally with most of the posterior portion being obscured by the pterotic; in *Gillicus* the fossa opens laterally and is not obscured at all; (8)in *Gillicus*, the subtemporal fossa is ovate in shape and proportionally smaller than the diamond shaped fossa found in *Cooyoo*; (9) in *Cooyoo*, the frontals bear strong curved ridges; comparable ridges are very weak in *Gillicus*; (10) in *Gillicus*, the ethmoid is club shaped, while in *Cooyoo* it ends in a rounded beak; and (11) in *Gillicus*, the sphenotics are forward directed hooks, while in *Cooyoo* they are simple, truncated points.

Main differences between *Cooyoo* and *Cladocyclus* are: (1) the parietals of *Cladocyclus* extend further forward down the midline of the neurocranium than those of *Cooyoo*; (2) the frontals of *Cladocyclus* do not, as in *Cooyoo*, exhibit curved ridges or a laterally extended shelf; (3) the ethmoids are broader and more rounded in *Cladocyclus* than in *Cooyoo*; (4) the sphenotics of *Cladocyclus* exhibit a posteriorly directed hook not seen in *Cooyoo*; (5) *Cladocyclus* exhibits an 'L'-shaped preopercular which tapers dorsally ending in a truncated point quite distinct from the broad, blunt, dorsal margin found in *Cooyoo*; (6) in *Cladocyclus* the premaxillaries appear to be proportionally shorter antero-posteriorly than those of *Cooyoo*; (7) the pterotics in *Cladocyclus* show an undulating suture with the frontals; in *Cooyoo*, this suture is straight; in addition, the pterotics of *Cladocyclus* do not appear to obscure the posterior portion of the hyomandibular fossa; (8) the epiotic crests of *Cladocyclus* are much smaller than those in *Cooyoo*, where the epiotic crests extend almost to the posterior margin of the supraoccipital crest; in *Cladocyclus*, the epiotics seem to be only half the antero-posterior length of the supraoccipital crest.

Of the other two genera, *Xiphactinus* and *Ichthyodectes*, the following comparison reveals that *Cooyoo* shows affinities with both genera but is sufficiently distinct from each to warrant separate generic status.

Comparison of *Cooyoo* with *Xiphactinus* reveals the following significant differences:

(1) the supraoccipital crest in *Xiphactinus* and *Cooyoo* commences on the parietals and exhibits a gradual rise from the dorsal surface of the neurocranium. The two genera differ significantly in the mean angle of flexure of this rise. In *Xiphactinus*, the mean angle of flexure is 30°. In *Cooyoo*, the angle is significantly less, the mean being only 15° (5 specimens).

(2) the relative height of the epiotic crests compared to that of the supraoccipital crest differs between *Xiphactinus* and *Cooyoo*; in *Xiphactinus*, the epiotic crest is approximately one-third the height of the supraoccipital crest; in *Cooyoo*, the relative height of the epiotic crest is only approximately one-quarter the height of the supraoccipital crest.

(3) the fused parietals of *Xiphactinus* exhibit 'An elongate cluster of small knobs...' (Bardack 1965, p.37) but the parietals in *Cooyoo* are unornamented. The construction of the parietals in *Xiphactinus* and *Cooyoo* is similar. In both, the parietals extend posteriorly some distance on either side of the supraoccipital crests. In *Cooyoo*, the parietals also form the anterior portion of the epiotic crests.

(4) the frontals in *Xiphactinus* are quite distinct from those in *Cooyoo*; in *Xiphactinus*, the dorsal surface of the frontal exhibits a broad shelf extending laterally above the orbit; the frontals of *Cooyoo* dorsally exhibit distinct ridges commencing at the base of the parietals and curving anterolaterally to form the dorsolateral margin of the frontals above the orbit.

(5) the ethmoids have been obscured or damaged in all known specimens of *Cooyoo*; thus, only a general comparison is possible with those of *Xiphactinus*; it seems that the ethmoids in *Cooyoo* terminate anteriorly in a "beak" contrasting with the rounded anterior margin in *Xiphactinus*.

(6) the sphenotics in *Cooyoo* and *Xiphactinus* are similar in shape; however, in *Xiphactinus*, they are orientated lateroventrally, while in *Cooyoo* they are directed laterally.

(7) the hyomandibular fossa also differs significantly in the amount that this fossa is obscured by the pterotics; in *Xiphactinus*, the fossa appears to open laterally, with the pterotic only forming the roof of the fossa and apparently not obscuring the opening of the fossa; in *Cooyoo*, the opening of the hyomandibular fossa faces ventrally; viewed laterally, the hyomandibular fossa is almost totally obscured; additionally, the fossa is not, as in *Xiphactinus*, horizontal; it slopes

obliquely from dorsal to ventral anteroposteriorly across the lateral surface of the neurocranium in *Cooyoo*.

(8) in *Xiphactinus*, the subtemporal fossa is quite large and rectangular, approximately two-thirds the length of the hyomandibular fossa in size, and is located below the middle of the hyomandibular fossa; the prootic-intercalar bridge forms the ventral margin of the fossa; the size of the fossa in *Cooyoo* is comparable to that found in *Xiphactinus*; however, its rhomboidal shape gives it a distinctly different orientation to that in *Xiphactinus*; in *Cooyoo*, the prootic-intercalar bridge forms the posterior ventral edge of the fossa and consequently, lies at an angle to the horizontal, tilting up posteriorly; this is quite distinct from the horizontal orientation of this bridge in *Xiphactinus*.

(9) in *Xiphactinus*, the lateral temporal fossa is confined to the pterotic and is formed as a depression just above the hyomandibular fossa; the dorsal rim of this depression rises gently from approximately the midpoint of the hyomandibular fossa to end just before the midpoint of the suture between the pterotic and the frontals. Posterior to the point above the hyomandibular fossa where this edge begins to slope upward, the rim flexes downward and then up again so that the pterotic forms a wing just above the middle of the hyomandibular fossa. The lateral temporal fossa in *Cooyoo* is very strongly developed, the roof of the fossa extending forward from the base of the pterotic up onto the frontals. The wing, formed by the pterotic above the hyomandibular fossa, completely obscures the posterior half of the fossa.

(10) the parasphenoid differs between *Cooyoo* and *Xiphactinus* in two main ways. Firstly, the amount of flexure exhibited between the otic and orbital sections of the bone is different, with *Xiphactinus* exhibiting a mean flexure of 160°, considerably more than the mean of 149° in *Cooyoo*. Secondly, the relative position of the division of the basisphenoid differs between *Xiphactinus* and *Cooyoo*; in *Xiphactinus*, this division occurs below the posterior end of the prootic, while in *Cooyoo*, it is below the anterior end of the prootic.

(11) the premaxillary is only present in a single specimen of *Cooyoo*, suggesting its attachment to the maxillary was weak; the premaxillary is roughly rectangular with a curved alveolar border bearing 6 alveoli and at least 4 teeth. In *Xiphactinus*, the premaxillary is ovate, with a straight dental margin bearing 5–6 alveoli, usually containing 2 teeth (Bardack 1965); it is reported as being firmly attached to the maxillary (Bardack 1965).

(12) the size of the maxillary teeth and the number of alveoli differs between the genera. In *Xiphactinus*, the teeth are large and variable in size, 1–4cm, while the average number of alveoli is 32; the teeth of *Cooyoo* are much smaller, having a mean size of 4mm, usually with little variation in size; the number of alveoli, 34, is similar to *Xiphactinus*.

(13) comparison of the hyomandibular apparatus reveals a number of differences, namely: in *Xiphactinus*, the mesopterygoid forms about one-third of the margin of the orbit, compared to *Cooyoo* in which it forms approximately one half the margin of the orbit; in *Xiphactinus*, the dorsal margin of the ectopterygoid, adjoining the metapterygoid, is straight and on the same line as the dorsal margin of the quadrate; in *Cooyoo*, this margin curves gently upward posteriorly, suddenly dropping down where the ectopterygoid meets the quadrate; and in *Xiphactinus*, the palatine head exhibits laterally directed flanges, which are absent in *Cooyoo*.

(14) the dorsal margin of the preopercular in *Cooyoo* and *Xiphactinus* differ in being blunt in *Cooyoo* and stepped in *Xiphactinus*.

Comparison of *Cooyoo* with *Ichthyodectes* reveals the following significant differences.

(1) the supraoccipital crest rises much more sharply above the surface of the neurocranium in *Ichthyodectes* (mean angle of flexure 39°) than in *Cooyoo* where the mean angle of flexure is only 15°

(2) the fused parietals in *Ichthyodectes* do not exhibit the posterior extensions which form the bases of the epiotic crests in *Cooyoo*

(3) the frontal ridges in *Ichthyodectes* are less distinct, being somewhat flattened and curve the opposite way to those in *Cooyoo*.

(4) the sphenotics in *Ichthyodectes* are anteroventrally directed with a sub-triangular shape, laterally, quite distinct from the truncated point in *Cooyoo*.

(5) the posterior end of the hyomandibular fossa in *Ichthyodectes* is partially obscured by a wing of the pterotic; the fossa opens laterally and is orientated parallel to the horizontal. This is quite different from the almost totally obscured, ventrally opening, obliquely orientated fossa in *Cooyoo*.

(6) the subtemporal fossa in *Ichthyodectes*, compared to *Cooyoo*, is proportionately smaller, approximately one-third the length of the

hyomandibular fossa; it is different in shape, being basically ovate in *Ichthyodectes* and rhomboidal in *Cooyoo*; and it differs in the orientation of the prootic bridge, which is horizontal and bounds only the posterior half of the ventral margin of the fossa in *Ichthyodectes*, in *Cooyoo*, it is slanted, forming the posteroventral corner of the fossa.

(7) the lateral temporal fossae are not as strongly developed in *Ichthyodectes* as that in *Cooyoo*.

(8) the parasphenoids in *Cooyoo* and *Ichthyodectes* differ in the relative position of the division which, in *Ichthyodectes*, occurs below the middle of the prootic, whereas in *Cooyoo*, it divides below the anterior end of the prootic; also, in *Ichthyodectes* the ventral surface is flat, while in *Cooyoo* it is curved.

(9) the maxillary teeth in *Ichthyodectes* (mean size of 8mm) are larger than those in *Cooyoo* (mean size 4 mm) while the average number of alveoli in *Ichthyodectes* (mean number 48) is higher, compared with the 34 in *Cooyoo*.

(10) the preoperculars in *Ichthyodectes* and *Cooyoo* differ in the nature of their dorsal margins; in *Cooyoo*, the margin is blunt, while in *Ichthyodectes* it narrows to a sharp point.

(11) the number of fin rays in the pectoral fin in *Ichthyodectes* and *Cooyoo* is different. *Ichthyodectes* possesses 11 fin rays while *Cooyoo* possesses 9.

DISCUSSION

The ichthyodectiform genera *Ichthyodectes*, *Gillicus*, *Cladocyclus* and *Xiphactinus* represent a group of closely related Mesozoic fish (Bardack 1965; Patterson and Rosen 1977; Bardack and Sprinkle 1969). *Cooyoo australis* is clearly closely related to this group. A comparison of its various characteristics shows a closer relationship to *Ichthyodectes* than any other ichthyodectiform genus including *Xiphactinus*, the genus in which it was originally placed. However it is also shown that *Cooyoo* differs sufficiently from both *Xiphactinus* and *Ichthyodectes*, to justify its removal to a separate genus.

The most important features separating *Cooyoo* from both *Xiphactinus* and *Ichthyodectes* are:

1) The angle of rise of the supraoccipital crest;
2) The shape of the frontals,
3) The form of the sphenotic;
4) Size, shape and orientation of the hyomandibular;
5) Shape of the premaxillary; and
6) Size of the maxillary teeth.

The significance of these differences is emphasised when the characters which have been used to diagnose other ichthyodectiform genera are examined. Characters used include dentition, degree of flexure of the parasphenoid, form of maxillary and dentary bones, form of the palatine head and presence or absence of ornament on the parietals (Bardack 1965). The character differences listed above are thus considered sufficient to support the placement of this species into a new genus.

The material of *Cooyoo australis* examined in this study showed little morphological variation between specimens. This is in contrast to the findings of Patterson and Rosen (1977) who observed significant variation between specimens of *Cladocyclus*. Patterson and Rosen (1977) felt unable to determine whether these differences were sexual, specific or generic '... because of the inadequacy of our sample, and because of absence of comparable information for other ichthyodectiform "genera".' (Patterson and Rosen 1977). The fact that no significant morphological variation was observed among specimens of *Cooyoo australis* suggests that the variations observed by Patterson and Rosen (1977) in *Cladocyclus* are not due to sexual dimorphism but probably represent at least specific differences.

The problems of assessing the significance of morphological variation is compounded in most cases by paucity of material. This is probably the main reason that no attempt has yet been made to rank the importance of morphological differences observed within the ichthyodectiform group. The need for such a study is emphasised by the fact that most ichthyodectiform genera are monotypic. Additionally in the few genera in which more than one species is recognised, the species are based on geological or geographic distribution (Bardack 1965; Patterson and Rosen 1977).

Allowing for the factors mentioned above it is concluded that while it has been shown that *Cooyoo australis* shares more characters with *Icthyodectes* than *Xiphactinus*, it has also been demonstrated that *Cooyoo australis* possesses sufficient morphological distinctiveness from both these genera to warrant the placement of it into an independent genus.

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